THE ART OF FEIGNING DEATH — THANATOSIS IN *EUPLOEA* (DANAINAE) AND OTHER APOSEMATIC BUTTERFLIES

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Introduction

Some years ago in the Nilgiri mountains of southern India I did experiments with Danaid butterflies which I had hoped to incorporate into a more general review of the feigning of death among butterflies. Geographical considerations make it unlikely that I shall be able to complete this review in the foreseeable future and the results of my observations in South India are given here, together with a few general remarks. The art of feigning death has been called *thanatosis* (after the Greek for death), and this term will be used here as a convenient short-hand.

The case of *Euploea core* and *E. sylvester*

Among butterflies, thanatosis is best developed in the Nymphalid subfamily Danainae, and among the Danainae it seems best developed in the genus *Euploea*. These are butterflies that are unpalatable to many vertebrate predators, most evidence being in respect of birds. In South India, two similar species were readily available (*E. core* Cramer and *E. sylvester* Fabricius). Their behaviour and re-action patterns did not differ so the results from these two species are pooled.

When a member of either sex of one of these species is handled, by holding the wings and touching the body, the following behaviour is invariably seen:

1. The abdomen is strongly curled downwards. In the male the yellow abdominal hair pencils are extruded. They emit a very pleasant smelling pheremone, the smell of which is readily evident to the human nose and varying from species to species. The female also has yellow patches on the ventral side of the tip of the abdomen, almost as if they were "mimics" of the male hair pencils. This is suggestive that the extrusion of the hair pencils are also intended to have a startling effect. The abdomen of a Danaid is not visible in its normal resting posture.
2. The legs are tucked tightly against the thorax, so that getting a grip even with a pair of tweezers is difficult.
3. The forewings are moved strongly forwards in relation to the normal resting posture, probably to expose as much of the warning colour pattern as possible.
4. The butterfly now rests inert in this position as long as it is still being manipulated, even lightly.
5. Once the specimen is released and laid on a flat surface, the hair pencils are gradually retracted, and the abdomen slowly straightens out, again becoming covered by the anal fold of the hindwings.

6. The forewings are gradually drawn back, significantly decreasing the total exposed surface. In the rare cases where the wings were held slightly open in the preliminary phases, they now close tight.
7. After a variable period of time, the butterfly will start moving its antennae. Shortly after that it rights itself abruptly, usually flying off immediately it is upright.

By and large this sequence was executed also by other Danaid genera tested in South India, but the extrusion of the hair pencils was infrequent in the genera *Danaus* (two species), *Parantica* (two species), and *Idea* (one species); two *Tirumala* species extended the hair pencils in about half of all tests. These species tend to have grey or brown hair pencils, not the brilliant egg-yolk colour of the *Euploea,* and may therefore have less of a startling effect.

Experiments in the Nilgiri Mountains

In the Nilgiri Mountains I brought back to my house a few live, papered Danaids after each of my collecting trips (April-October 1986). They were released in a room till the following morning. When it was fully light and the butterflies began flying spontaneously, they were caught by holding the discal area of the forewings with two fingers. They were then given a very light pinch on the thorax with two finger tips. When the abdomen immediately began to curl, it was rubbed lightly with the tip of a finger nail. This was meant to simulate a tentative predator attack. The butterfly was then placed on a sheet of newspaper in full light, but not in direct sunlight. The amount of time spent inert was noted:

Table 1. Time spent in thanatosis by two *Euploea* species.

Seconds	Males	Females	Total	Percent
— 30	2	6	8	9.1
31 — 60	7	9	16	18.2
61 — 120	7	6	13	14.8
121 — 180	11	4	15	17.0
181 — 240	5	4	9	10.2
241 — 300	5	2	7	8.0
301 — 600	4	4	8	9.1
601 — 900	7	1	8	9.1
900 + *	4	0	4	4.5
Total	52	36	88	100.0

* Actuals were 2280, 2220, 1800, and 1100 seconds, i.e. between 38 and 18 minutes.

It will be seen from the table that only a few specimens flew away more or less immediately after being handled, the majority of these staying almost 30 seconds. Twenty percent of the sample were inert for between 30 seconds and a minute. Half the sample was inert for between one and five minutes, while the remaining quarter of the sample spent more than five minutes in thanatosis, with a maximum of 38 minutes in a male of *Euploea core*. The median time spent in thanatosis was two to three minutes. There is a tendency for females to spend slightly less time in thanatosis than males, with a maximum of 12 minutes in *E. core*. I obtained very similar results with about 100 *E. core* in New Delhi, but the notes are not available.

Smaller numbers of other Danaid genera show a similar pattern, with a specimen of *Tirumala septentrionis* Hewitson at a maximum of 30 minutes and a *Danaus genutia* Cramer at 17 minutes.

Why thanatosis?

The purpose of thanatosis seems to be to stop a predator attack before serious damage has been done, in order that (1) the prey may escape, since the predator believes it to be subdued; (2) the prey has the opportunity to deploy some other defensive mechanism; or (3) the predator has time to discover that the prey is inedible or unpalatable.

Some harmless snakes and lizards fall in the first category, flipping over on their backs, lying inert, and then suddenly making a dash for it. The click beetle feigns death in order to deploy its splendid escape mechanism and falls in the second category.

Danaid butterflies are usually unpalatable or even noxious, not least in respect of insect-hunting birds (many examples are given by Ackery & Vane-Wright 1984). They therefore fall into category (3). The median time of two to three minutes in thanatosis would appear to be a suitable length of time to ensure that the predator has abandoned the attack. Two naîve kittens were given *Danaus chrysippus* and various unpalatable moths in Botswana; most survived a considerable amount of pawing, in some cases feigning death for more that an hour, finally being completely ignored by the kittens.

The advantages of thanatosis in Danaid butterflies are enhanced by their being much tougher than most other butterflies. It can be quite difficult to kill them with the traditional pinch of the thorax. This toughness combines with the neophobic approach to prey characteristic of many predators. They will swallow an unfamiliar prey item only after careful assessment and may well recognise a Danaid as unpalatable before lasting damage has been done.

A quick survey of the Lepidoptera will show that thanatosis *and* toughness of the integument (especially the thorax) is largely, perhaps exclusively, limited to unpalatable species of the type that are models in mimicry complexes: *Pachliopta, Atrophaneura* (Papilionidae); *Delias,*

Pereute (Pieridae); many Acraeinae, Ithomiinae, Heliconiinae, *Cethosia* (Nymphalidae); many Zygaenidae, Ctenuchidae, and Arctiidae (Heterocera).

I cannot recall any butterfly which displays thanatosis for which there is not good evidence that it is also unpalatable. There are, however, unpalatable butterflies which have not developed strong integuments, especially in the Pieridae, but this seems to be mainly in genera where only some species are unpalatable, and which appear less specialised than those mentioned above (*Pieris brassicae* Linne being a good example).

On the other hand, among the butterflies, I know of only two species which are apparently palatable and yet have tougher integuments than even the Danainae. One is the virtually indestructible *Thaduka multicaudata* de Niceville (Lycaenidae: Theclinae). Even the strongest pressure on the thorax with a pair of nails, accompanied by audible cracking of the thorax, fails to do damage. In the evening it will fly out seemingly undamaged from its paper. *Bibasis sena* Moore (Hesperiidae: Coeliadinae) is almost as tough. They are, however, very much exceptions to the rule, and their toughness is not shared with their closest generic relatives in southern India. There may be more examples among the Heterocera (e.g. the Cossidae).

Conclusion

Thanatosis, in various guises, is common throughout the animal kingdom. However, at least among butterflies it normally seems to have co-evolved with unpalatability *and* the development of a particularly tough integument. Since all three elements have co-evolved independently in a number of different butterfly families their combination appears to have particularly strong survival value.

Reference

Ackery, P. & Vane-Wright, R.I., 1984. *Milkweed butterflies*. British Museum (Natural History). London.

Sedina buettneri Her., Blair's Wainscot (Lep.: Noctuidae) in Kent.

A single male *S. buettneri* was caught in the Rothamsted Insect Survey (R.I.S.) light trap at Lydd, Kent (Site No. 462, OS grid ref. TR 044 203) on 2.x.1987. *S. buettneri* was known to occur at Freshwater Marsh, Isle of Wight, from 1945 to 1952 (Skinner, 1984). Its history at Freshwater, and accounts of its biology, are given by Blair (1946; 1950; 1951), Tams (1946), Robinson (1950) and Heath & Emmet (1983).

There were no further records of this species in Britain until an individual was caught at mercury vapour light by Tweedie (1967) at Playden, near Rye, E. Sussex on 14.x.1966. There were few primary migrant Lepidoptera recorded during October 1966 (B. Skinner, pers. comm.). Following this record, B. Skinner and K. Satler made an extensive search of Romney and